

# SIZE-SELECTIVE TRANSPORT OF SHELLS BY BIRDS AND ITS PALAEOECOLOGICAL IMPLICATIONS

by GERHARD C. CADÉE

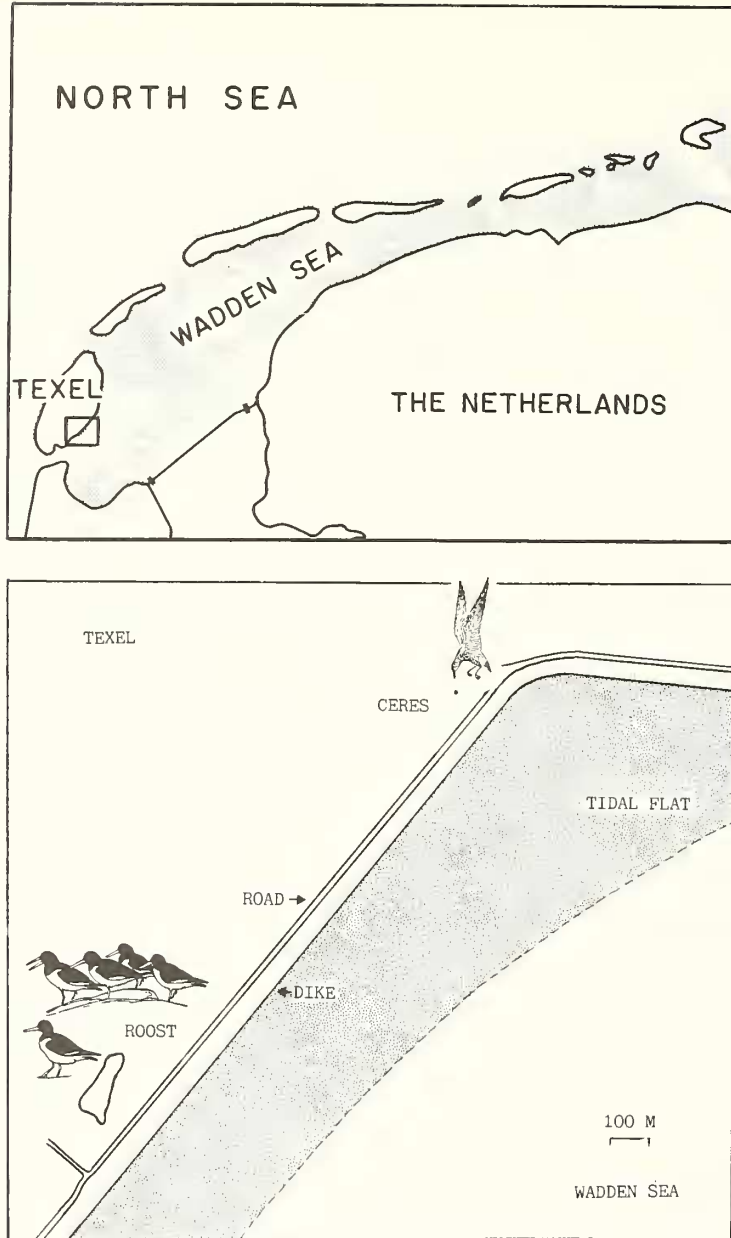
**ABSTRACT.** Size-selective transport of shells is demonstrated in the Dutch Wadden Sea for the Herring Gull (*Larus argentatus*) and the Oystercatcher (*Haematopus ostralegus*): only larger shells were transported. Size-selective transport of shells by predators is one of the taphonomic processes altering the size-frequency distribution of shells in the death assemblage: it results in mortality not recorded in the death assemblage forming where the animal lives. Such transport will occur particularly in intertidal areas. It hampers the use of size-frequency distribution for studies of population dynamics in fossil assemblages.

SIZE-FREQUENCY distribution in a fossil assemblage is dependent on the interplay of growth rate, mortality rate, taphonomic processes, and usually also time averaging (Cummins *et al.* 1986). It is therefore like an equation that cannot be solved because there are too many unknown variables. Nevertheless, palaeoecologists have tried to use size-frequency distributions to extract data on transport or population dynamics from fossil assemblages ever since the early stimulating papers by Boucot (1953) and Kurtén (1953) (see Hallam 1972; Cadée 1968, 1982; Cummins *et al.* 1986 for other references).

The formation of a death assemblage is the initial step in the creation of a fossil assemblage. During this step the skeletal components of preservable organisms are subjected to such taphonomic processes as dissolution, breakage, bioerosion, abrasion, transport, and time averaging (shell condensation), all of which may alter the size-frequency distribution (Cummins *et al.* 1986). The study of these 'biostratinomic' processes has a long history (see Schäfer 1962; Müller 1976, 1979).

The importance of predation in producing shell fragments has been stressed by, among others, Schäfer (1962), Cadée (1968), and Trewin and Welsh (1976). In this paper I will concentrate on transport of shells by predators which represents a process of mortality not recorded in the death assemblage forming in the localities where the animals live. After 20 years of problems with punctured bicycle tyres on my way to the laboratory due to shell-smashing activities of gulls, I learned to see this activity as a mechanism by which shells are transported from the intertidal area to land. Do these gulls select shells of a certain size? Such a selection was reported by Zwarts and Drent (1981) for the Hooded Crow which uses the same smashing method. Moreover, a nearby roost of Oystercatchers offered the opportunity to study transport of *Mytilus edulis* to the roost on land and possible size selection by this species. Such a transport was first reported by Leopold *et al.* (1985) and found to be non size-selective.

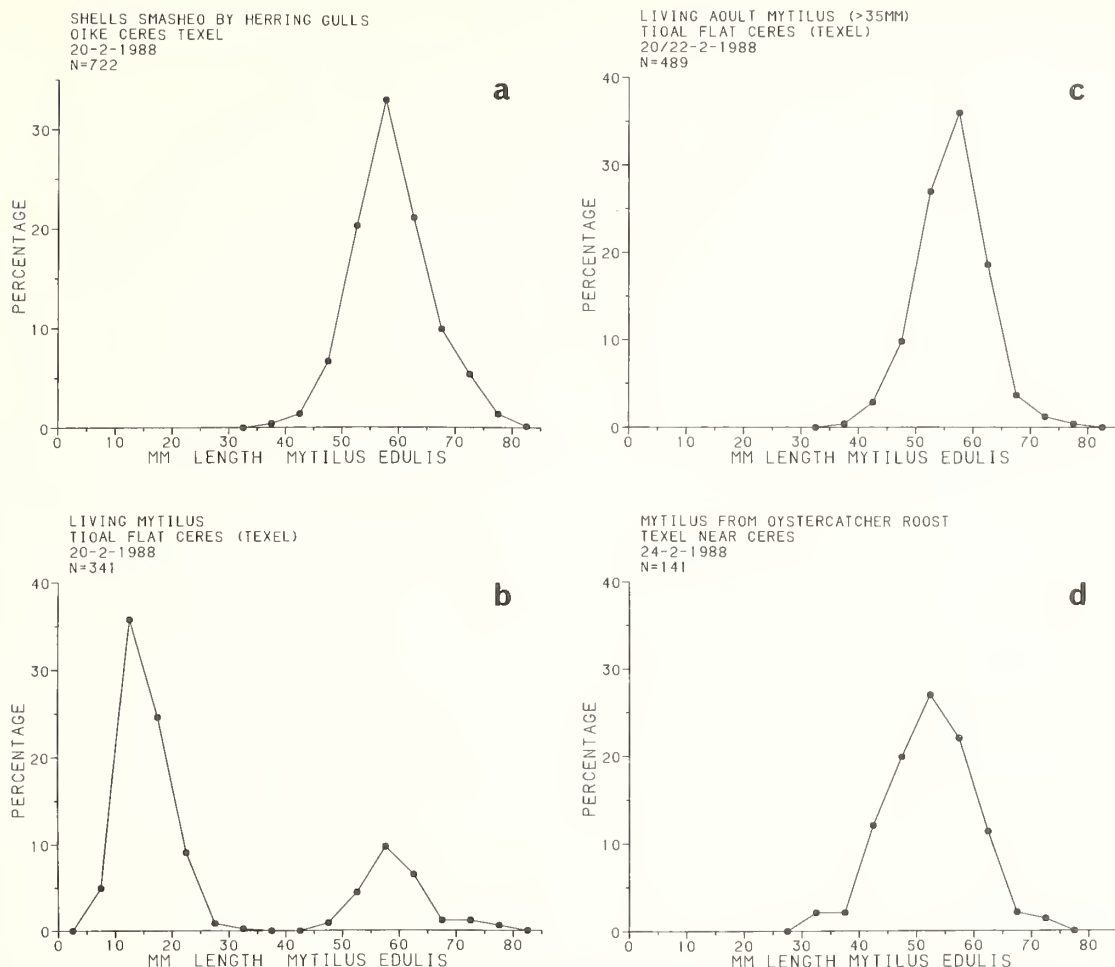
Transport of shells from sea to land by birds foraging in the intertidal area has been reported repeatedly. Most data pertain to gulls (Sunkel 1925; Schwarz 1932; Teichert and Serventy 1947; Remane 1951; Goethe 1958; Schäfer 1962; Barash *et al.* 1975; Siegfried 1977; Kent 1981) and the palaeoecological importance has been stressed: marine shells transported to a terrestrial habitat may pose problems in the correct interpretation of the terrestrial palaeoenvironment. Transport of shells from the intertidal area, however, will also alter the death assemblage of shells left behind, particularly if such a transport is quantitatively important. If such transport is size selective, it will influence the size-frequency distribution of the death assemblage, presenting problems in the use of size-frequency distribution in palaeoecology (e.g. for population dynamics).



TEXT-FIG. 1. Location of tidal flat (stippled), shell-smashing locality of Herring Gulls and Oystercatcher roost studied.

### OBSERVATIONS

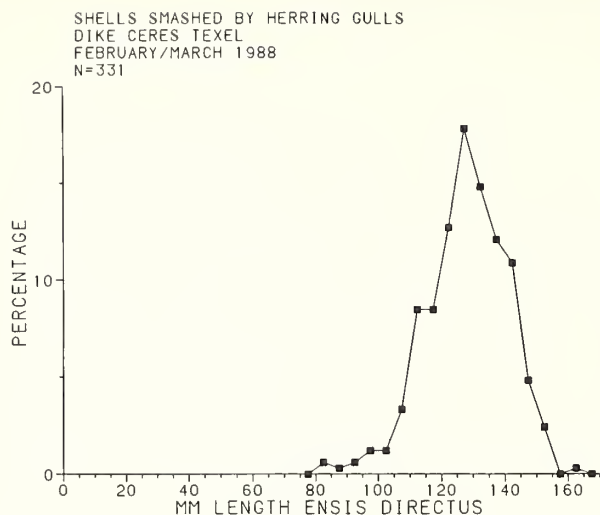
A large sample was collected in February 1988 of fresh *Mytilus* shells recently dropped by Herring Gulls (*Larus argentatus*) on the dike bordering a tidal flat area of the Dutch Wadden Sea along the south-east coast of Texel, near polder Ceres (text-fig. 1). Most shells still contained some adherent soft tissue. Shell length was measured to the nearest millimetre and the resulting



TEXT-FIG. 2. Size-frequency distributions of *Mytilus edulis* shells. *a*, dropped by Herring Gulls; *b*, living population; *c*, living adults only; *d*, from Oystercatcher roost. Size classes 5 mm, all measurements to the nearest mm.

size-frequency distribution is given in text-fig. 2*a*. Gulls collected these mussels from mussel-beds on the tidal flat bordering the dike. The living mussel population was sampled there at a number of localities within this feeding area for size-frequency distribution measurement (text-fig. 2*b*). A comparison of the two size-frequency distributions reveals a marked difference: the size-frequency distribution of the living population is bimodal, that of the dropped shells shows a normal distribution. The smaller mussels, all year class 1987, were well represented in the living population but absent in the assemblage of shells transported by gulls. Average size and standard deviation were  $25.9 \pm 19.4$  and  $58.7 \pm 6.9$  mm for the living and the dropped population, respectively. This clearly indicates a size selection by gulls. Only the larger mussels, of older year classes, were transported.

To measure the size-frequency distribution of this older living population more exactly, a larger sample was collected of only older *Mytilus* (text-fig. 2*c*). Size-frequency distributions of older living *Mytilus* and shells transported to land and smashed are very similar (average and standard



TEXT-FIG. 3. Size-frequency distribution of *Ensis directus* shells smashed by Herring Gulls.

deviation respectively  $56.2 \pm 5.8$  mm and  $58.7 \pm 6.9$  mm). Although the difference of 2.5 mm is statistically significant (t-test), this most probably does not indicate size selection by gulls but spatial variation within the mussel population and the difficulty in collecting exactly the population which the gulls were feeding on.

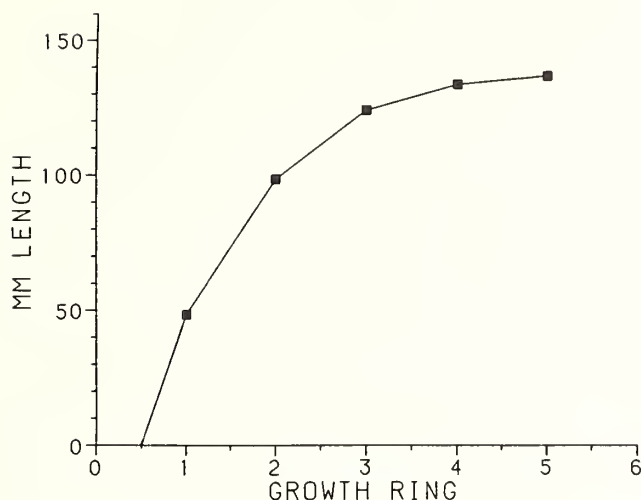
Smashing activity of gulls occurs the year round but shows a seasonal variation with a peak in winter. The condition index (ratio meat weight: shell volume) of *Mytilus* is lower in this period than in summer (Zandee *et al.* 1980) because phytoplankton concentration is lowest in winter (Cadée and Hegeman 1979). For the same amount of food a gull has to collect in February/March twice as many *Mytilus* as in August/September. So it is not food quality which makes the gulls select *Mytilus* particularly in winter, but probably a lower availability of other food types.

Between the smashed *Mytilus* shells on the dike a number of American razor clams (*Ensis directus*) were found, also with adhering soft tissue, which apparently were smashed by Herring Gulls too. Subsequently, such shell smashing of *Ensis* by Herring Gulls was indeed observed. *E. directus* is a recent immigrant in the Dutch Wadden Sea (Essink 1985). Size-frequency distribution of these shells also showed that only large specimens were transported (text-fig. 3). Not all *Ensis* shells had been broken when dropped. Apparently some shells opened without breaking. Kent (1981) reports the same for *Argopecten* dropped by Herring Gulls. Because of the difficulties in sampling razor clams adequately (they are fast movers in the sediment), I did not try to collect a representative sample of the living population for comparison. Instead growth was measured using the growth rings on the shells to estimate the age of the transported razor clams. Measurements of annual growth rings are given in text-fig. 4. Length increase is comparable to that found by Swennen *et al.* (1985) in the German part of the Wadden Sea. From these growth rate data it is concluded that Herring Gulls dropped only older *Ensis* shells with two to four winter rings.

*E. directus* is a recent addition to the food resources of birds in the Wadden Sea (Essink 1985; Swennen *et al.* 1985). *E. directus* was an important food item for Herring Gulls and Oystercatchers (*Haematopus ostralegus*) foraging at extreme low tide on the tidal flat studied. The Herring Gulls did not collect all these razor clams and mussels themselves, but stole some from Oystercatchers ('kleptoparasitism'). Swennen *et al.* (1985) observed that some Oystercatchers have specialized in feeding on *E. directus*, a new kind of prey in the Wadden Sea where before its introduction no razor clams occurred. Herring Gulls have also adapted to this new prey which they collect when swimming above the flat at low tide and in water depths of 10 to 20 cm. The Herring Gulls used the smashing method for *Ensis* only sporadically; in most cases they were able to feed on *Ensis* without smashing.

GROWTH CURVE *ENSIS DIRECTUS*  
TIDAL FLAT CERES TEXEL  
FEBRUARY/MARCH 1988

TEXT-FIG. 4. Growth curve of *Ensis directus* from tidal flat near Ceres.



*M. edulis* shells collected on the Oystercatcher roost showed a size distribution comparable to that of the shells dropped by Herring Gulls: the smaller *Mytilus* of year class 1987 were not transported, only older larger shells were found (text-fig. 2d). They were somewhat smaller (average and standard deviation  $52.3 \pm 7.4$  mm) than the older shells in the living population. This may be due to the fact that the Oystercatchers roosting here feed over a larger area of the tidal flat, which was not adequately sampled. Inspection of other mussel-beds in this tidal flat area indeed indicated such differences; in some places also the small mussels of the 1987 year class were almost lacking. Another explanation could be that the *Mytilus* taken to the roost are the last ones the Oystercatcher was able to collect before the feeding area became submerged. *Mytilus* living higher in the intertidal zone are smaller because they have a shorter feeding period per tide (Dare 1976).

## DISCUSSION

A number of methods by which birds transport shells have been described in the literature, particularly concerning the Herring Gull. Shells, some not used as food by this bird, are transported to the nest and used as 'decoration' (Goethe 1937). Males present quantities of bivalves to the female (Tinbergen 1953; Goethe 1958), and these bivalves largely remain uneaten and intact near the nest. Some small shells are brought to the breeding colony as food for chicks, but according to Spaans (1971), fish form the main food for chicks. Quantitatively, however, transport of shells for these purposes will be small compared with transport of bivalves as food for (sub)adults. Smaller bivalves are ingested whole when small (9–23 mm length; Harris 1965; Spaans 1971) and broken in the muscular stomach. Their remains are dropped as faeces or regurgitated as pellets (cough balls) on land, on roosts, or in the breeding colony. Remane (1951) calculated this transport to be 1450 tons per year for the German coast. Since then the number of Herring Gulls has increased considerably (Smit and Wolff 1981).

Remane (1951) did not include the smashing of shells by Herring Gulls in his estimates. Larger shells are first broken by smashing (Oldham 1930; Tinbergen 1953; Goethe 1958; Ingolfsson and Estrella 1978; Kent 1981; personal observations) and the meat is extracted leaving the shells behind. Shells for smashing are taken some 4 to 10 m in the air and dropped on the tidal flat, but sometimes they are brought to dry land. Most successful are those birds that drop shells on a hard surface



(rocks, pebbly beach, artificial dike, road), but Herring Gulls do not select hard surfaces according to Oldham (1930) and Tinbergen (1953); moreover, hard surfaces are not always available (Kent 1981). However, Ingolfsson and Estrella (1978) found a marked preference for hard surfaces. I found that whereas some gulls seem to select the road or the hard surface of the dike, others dropped shells on the tidal flat, on grass, or even in water. Shells dropped on land break after being dropped one or several times. Oldham (1930) and Smit and Wolff (1981) report smashing of shells also for the Common Gull (*Larus canus*). For a number of species of gulls in other parts of the world the smashing method has been described (Teichert and Serventy 1947; Barash *et al.* 1975; Siegfried 1977; Kent 1981; Maron 1981), indicating its widespread occurrence among the larger gull species. The Hooded Crow (*Corvus corone cornix*) also displays this smashing method, but they confine themselves to bombing hard soils (Tinbergen 1953). Whereas only the older mussels were observed smashed (the smaller can be swallowed whole), without size selection among these older mussels, Kent (1981) found that his Herring Gulls showed a decided preference for smashing the largest available prey. Siegfried (1977) reports such a size selection among the larger shells for Kelp Gulls (*L. dominicanus*), as do Zach (1978) and Zwarts and Drent (1981) for the crows *C. caurinus* and *C. corone cornix* respectively.

Oystercatchers open shells (*M. edulis*, *Cerastoderma edule*, *Macoma balthica*, *E. directus*) with their strong beak and extract the meat without ingesting the shell (Tinbergen and Norton-Griffiths 1964; Norton-Griffiths 1967; Hulscher 1982; Swennen *et al.* 1985). Shells are left on the feeding area and usually no transport is involved except when Oystercatchers try to escape kleptoparasitism by gulls or other Oystercatchers (Leopold *et al.* 1985; and personal observations). However, Leopold *et al.* (1985) reported long-distance transport of shells by this bird from the intertidal feeding area to the high-tide roosts. This was confirmed by the finding of *Mytilus* shells at the roost on Texel. Leopold *et al.* (1985) did not find size-selective transport. This difference with the results presented herein can be explained by the differences in the size-frequency distribution of the living populations. The smaller *Mytilus* were almost absent in the living populations they studied (mean shell length, SD, and range given as  $37.9 \pm 7$  (20–62) and  $48.2 \pm 7.1$  (28–71) mm). The size selection observed in the current study on Texel agrees with size selection of mussels used for feeding as reported in the literature; Norton-Griffiths (1967) observed Oystercatchers to select larger mussels, none smaller than 16 mm being eaten. Zwarts and Drent (1981) found a peak in the living population of *Mytilus* at 10 mm length which was not consumed by the Oystercatcher. However, Zwarts and Drent also observed a size selection for larger shells from the older *Mytilus* population. Compared with the 'modal mussel' of 44 mm, the relative risk of a mussel of 50, 54, or 58 mm being consumed by an Oystercatcher was 3.6, 6.7, and 10.5 times as high, respectively. *Mytilus* transported to the roost do not show this size selection for larger shells (Leopold *et al.* 1985; this study). This could be due to the fact that they were taken from high in the intertidal zone (see above). Shell transport to the small roost on Texel studied here was far less important than that observed by Leopold *et al.* (1985) who estimated an annual transport of 1.3 tonnes of *Mytilus* shells on a large Oystercatcher roost.

Another example of a bird that transports shells in the Wadden Sea is the Eiderduck (*Somateria mollissima*). They collect their food by diving and therefore are also able to feed subtidally and on tidal flats during high tide. In the Dutch Wadden Sea this bird feeds largely on *Mytilus* and *Cerastoderma*. They ingest these molluscs entire and crush the shells in their muscular stomachs. The crushed fragments, most between 1.5 and 4 mm (Trewin and Welsh 1976), leave the birds as faeces. During low tide part of the eider population roosts on tidal flats, and in the breeding period eiders roost ashore near the nesting site, with only sick birds roosting ashore in winter (Swennen 1976). Most of the defaecation of the shell fragments occurs during roosting, and thus away from the feeding area, involving a transport of (fragmented) shells from the habitat where the molluscs lived. Eiderducks do select for size: they avoid eating the largest bivalves probably because larger prey offers a greater risk of internal injuries (Swennen 1976). The population of Eiderducks in the Dutch Wadden Sea (63 000 on average the year round) was estimated to consume 32 000 tonnes dry weight of flesh or  $1.2 \text{ g.m}^{-2}\text{.yr}^{-1}$ . More than 80% of this food consists of the bivalves mentioned

(Swennen 1976, 1981). As shell weight is about 15–20% of dry weight, this indicates a considerable and size-selective transport of shells by these birds of 3800–5100 tonnes per year, albeit as fragments. Compared with the total carbonate production of shells in the Wadden Sea (Beukema 1982) it amounts to c. 3%.

Fewer quantitative data are available on other birds in the Wadden Sea that feed size-selectively on molluscs and produce faeces and/or cough balls on land containing shell fragments. Examples of birds feeding mainly on molluscs are Shellduck (*Tadorna tadorna*), Common Scoter (*Melanitta nigra*), Curlew (*Numenius arquata*), and Knot (*Calidris canutus*), the latter taking mainly spat-size molluscs. A number of other birds in this area feed partly on molluscs (van der Baan *et al.* 1958; Swennen 1975; Smit and Wolff 1981).

Size-selective predation on the tidal flats is not confined to birds. During high tide, aquatic predators forage on the tidal flats (plaice, see Kuipers 1973, 1977; shore crab, see Klein Breteler 1976; shrimps, see van der Veer and Bergman 1987). From Kuipers' (1977) data it may be concluded that plaice transport shells (as fragments) from the tidal flat to the channels.

### PALAEOECOLOGICAL RELEVANCE

Hallam's (1972, p. 78) statement that no pronounced size-selective effects of predation have been clearly demonstrated in the fossil record is probably still correct. However, this illustrates only the difficulty in demonstrating such effects, not that they do not occur. Data from Recent environments indicate that size-selective predation is more the rule than the exception (see Daan 1973, Ursin 1973, and Kuipers 1977 for fish; van der Veer and Bergman 1987 for shrimps). Vermeij (1978) and Reise (1985) give examples of size-selective predation on molluscs. Size-selective transport by predators is demonstrated in this paper for the Wadden Sea where it might involve at least 5 to 10% of the total shells produced.

Size-selective transport by predators is probably best developed in intertidal areas where predators can feed during only part of the tidal period. All these predators show tidal migrations between feeding areas on the tidal flat and resting areas on land or in deeper water. It may also occur in subtidal waters visited for instance by predators during the night that return to deeper water during the day. Parrish (1987) gives examples of this 'guild of daily commuters' from the reef environment.

It will be clear that, although difficult to demonstrate in the fossil record, size-selective predation (including fragmentation and/or transport) may be significant enough to hamper the use of size-frequency distribution of fossils for studies in population dynamics; particular size groups may not be fully represented in the fossil assemblage. This supports the conclusion reached by Cummins *et al.* (1986) that the value of size-frequency distribution in fossils to assess a species' population dynamics is doubtful.

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